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# Blood Groups in the Study of Human Populations\*

## Introduction

WHEN A EUGENIST turns to the study of genetics I suppose that he thinks in terms mainly of those characters which can be described as advantageous or disadvantageous to the individual or to the human race. Unfortunately for the geneticists, but perhaps fortunately for the race, goodness, cleverness, good health and beauty are not simple genetical characters. In so far as they are genetically determined at all, each of them is the resultant effect of a very large number of different genes acting together. The same is true of all those characters of shape, size and colour by which we recognize and classify human beings. Almost the only characters of direct and obvious interest to the eugenist which are genetically simple are the congenital diseases, or at any rate the majority of them, and these fortunately are relatively rare.

The blood groups are genetically very simple, in this resembling congenital diseases, and the rules by which they are inherited have in nearly all cases been very fully worked out; they possess, moreover, the advantage that, the genotype having been determined once for all at the moment of conception, the adult phenotype develops almost completely by the time of birth and quite fully by the age of about one year, and thereafter remains fixed for life. A year or two ago one could have made this statement quite categorically, but it is now known that, in a few individuals in every hundred thousand or every million, the ABO blood-group phenotype, though not, of course, the genotype, is modified by disease. This is, of course, quite unimportant

in population studies, however important it may be from a medical point of view; the change moreover, is not one which would deceive a competent serologist who was aware of the possibility.

Nevertheless, the blood groups cannot be regarded simply as neutral markers like labels attached to individuals or populations from the outside. As we shall see later, the blood groups of individuals do, though to a minor degree, affect their health and fitness, and so these characters are involved in the processes of natural selection and of evolution. However, as a first approximation, we can regard the frequencies of the blood groups in a population as remaining unchanged from one generation to the next; so that they are, in fact, the most useful of all markers in studies involving ancestral relationships between populations, and calculations of the proportions in which the original components have entered into a hybrid race.

## Blood Group Testing

When I wrote the notes for this lecture I intended to describe very briefly how blood groups were determined. Having seen how many of my blood-grouping colleagues have come to support me by their presence, I feel somewhat embarrassed at this. Nevertheless, I feel sure that there are some of you who have not done any blood grouping, so I shall describe very briefly how the tests are done, in order to give some idea of what I am talking about when I refer to someone as being, for instance, group MN, or Rh-positive.

As you know, the blood consists of a great many components, of which the most abundant are the red corpuscles or red cells, which are microscopic reddish-coloured discs, and the

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\* A paper read at a Members' Meeting of the Eugenics Society on November 18th, 1959.

almost clear fluid in which they are suspended, the plasma. Although the red cells are so minute, being only  $1/3,500$  in. in diameter, each nevertheless contains many millions of chemical molecules, and this gives considerable scope for the development of a variety of those particular molecules which determine the blood groups. These chemically very complex substances, known as antigens, are situated on the outer skin of the cell, and something like sixty different blood group antigens are known, of which any one individual has perhaps a dozen or twenty.

Corresponding to each of the known antigens is a particular reactive substance (an antibody) which is contained in suitable testing fluids. These fluids usually consist of serum obtained from human beings or animals, or in certain cases of extracts of plants, but we shall for the moment treat them as empirical testing reagents without worrying about their origin. If a particular sample of red cells contains the antigen which corresponds to a given testing fluid, then, when the fluid is added to the cells, the latter, instead of remaining separate, alter their surface properties and stick to one another to form clumps. The essential blood-grouping test thus consists in adding separate portions of each blood sample to a variety of these testing fluids, and seeing whether the red cells go together in clumps.

### The Genetics of the Blood Groups

By carrying out such studies on the red cells of enormous numbers of human beings—for instance, there are in the literature the published results of over 6,000,000 ABO blood-grouping tests—and by carrying out such tests on members of known families, it has been possible to determine the way in which each of these antigens, or rather, the ability to make it, is inherited. It has thus been found, by testing many thousands of families, some for one or two antigens and some for large numbers of them, that these substances are the product of genes; in general one may say that each antigen is determined by a single gene. The same family studies have shown that these genes fall into eleven major independent genetical systems which we refer to as the blood-group systems. Within each system you may have

anything from two to perhaps a dozen distinct genes.

It would take me far too long to describe the genetics of each of the blood-group systems, but I must say a little more about the three systems with which we are mainly concerned in population and anthropological studies. First of all, the ABO system: as many of you know, there are four main blood groups, O, A, B and AB. These are the products of three different kinds of allelomorphic genes, O, A and B; each individual will, of course, have two such genes, alike or different, one received from each parent. This gives a possibility of six different genotypes, OO, AA, AO, BB, BO and AB. The reason why there are only four blood groups, or distinguishable phenotypes, is that AA and AO are indistinguishable, corresponding to group A, as are BB and BO, corresponding to group B. The other two genotypes, OO and AB, correspond, of course, to blood groups O and AB respectively.

Thus, when we have determined the blood group of an individual, there may still be some doubt as to the genotype. However, if we test a sufficiently large number of persons we can calculate the frequency of the three genes in the population as a whole. We do, in fact, frequently find it convenient to express the composition of a population not in terms of the blood groups, or phenotypes, but in terms of the genes.

One reason for doing this is that it reduces the number of mathematical variables. In the case of the ABO system the frequencies of four blood groups are reduced to those of three genes; moreover, the total frequencies of the latter add up to 100 per cent so that if you know the frequencies of A and B you can tell that of O, and there are thus really only two independent variables; if you plot on a graph the percentages of gene A in one direction, and those of gene B in the direction at right angles to it, the composition of any population can be expressed completely by means of a single point. As you will see later, we frequently represent and compare series of populations by means of graphs of this sort.

The Rh or Rhesus system is much more complex. I will not, however, weary you with its full, and indeed unfathomed, complexities, nor with the interminable controversies that have

been waged over them. I shall merely try to set out a relatively simple scheme which is widely accepted as being a fair approximation to the true state of affairs. Whereas the ABO groups are the expression simply of one pair of genes at corresponding loci on one pair of chromosomes, the Rh groups may be regarded as being due to a pair of *sets* of genes, each set occupying three closely adjacent loci on a chromosome, the loci being occupied respectively by gene D or d, by C or c, and by E or e. The linked sets of genes are represented by sets of symbols such as CDe cDe, cde, but for some purposes it is useful to express them in a sort of shorthand (which actually has priority to the three-gene system); the short symbols for the three examples just given are:  $R_1$ ,  $R_0$  and r, respectively. Persons who have at least one D gene are known as Rh-positive; those with two d genes as Rh-negative.

It is now known that the scheme just described is an over-simplification: there are certainly more than two possible allelomorphic genes for each locus (though each individual can have only two); there appear to be more loci than three; and each of the supposed simple genes may itself be complex; however, for most purposes the simple hypothesis of three adjacent loci is adequate. Because the genes on a single chromosome are so close together they are inherited *en bloc*. It is thought that if you were able to study many thousands of individuals from selected matings, as you can with mice, then, once in several thousand families, you would probably find that the process of crossing over had taken place, and that a block of genes present in a parent had not been passed on intact to a child. However, with the limited numbers of human families available for testing, no convincing exceptions have been found to the rule that each block is passed on intact. With the exception of little d, which is rather mysterious, each of the genes corresponds to an antigen, and each of the latter to an antibody present in a testing fluid, so that instead of a single reaction of a single chemical substance being passed on from generation to generation as with the ABO system, in the Rh system it is a set of chemical compounds, or a set of reactions, which is passed on.

The MN system is genetically similar in plan to the Rh; here there are two main closely linked loci, one occupied by gene M or N, the other by S or s. Again as with Rh, the complexity is certainly greater than is expressed by this simplified scheme. There are other allelomorphic genes that can be present at each of these two loci; there are certainly more than two loci—possibly five or more—and again the supposed genes may themselves be complex. For to-night, however, we shall keep to the simplified scheme.

There are eleven major blood-group systems; we have so far considered three. In most of the remaining cases the genetics are considerably simpler than in the ones I have described, but as each system is studied more and more closely, unsuspected complexities tend to appear.

### Blood Groups and Anthropology

I want to turn now to the application of these genes, considered as markers, to a variety of populations. When we study the distribution of the genes of the ABO, Rh and MN systems throughout the world, we find that the latter can be divided into seven or eight fairly distinct regions corresponding reasonably closely to the regions into which most physical anthropologists would divide it; within each of these areas there are relatively small variations in the frequencies of the genes of most of the blood-group systems, whereas between the areas there are frequently very much bigger differences. This is true, in particular, of the Rh and MN systems; but in the case of the ABO system, although the average frequencies are quite characteristic for each major area, there are very wide variations in frequency within each of the areas, even down to quite significant differences between adjacent counties in this country.

I have suggested, and I shall revert to this suggestion later, that the reason for this is that the ABO blood groups are subject to a much more rapid variation than the others by means of natural selection in relation to features of the environment. It is probable that the Rh and MN blood groups also are subject to natural selection, but, if so, at a much slower rate, so that the inter-marriage which takes place between people from different parts of Western Europe, for example, is sufficient to keep Rh and MN

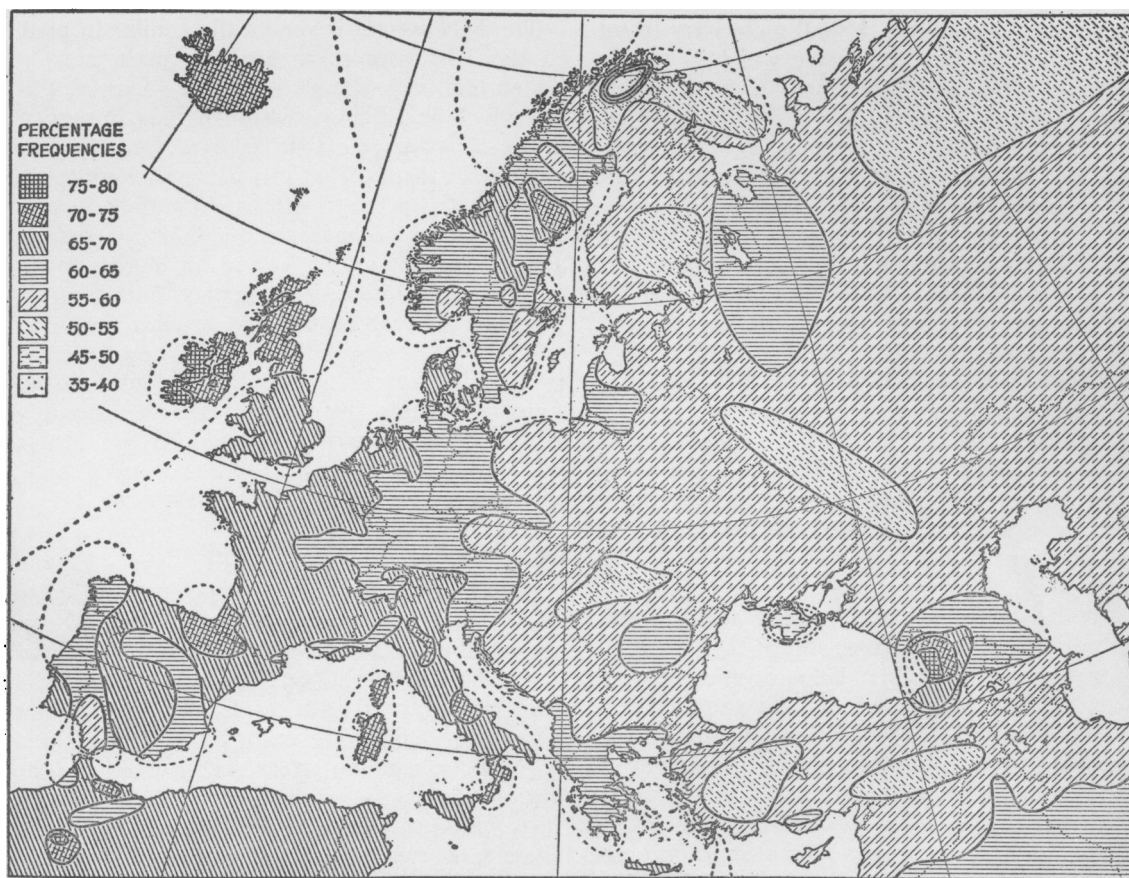


FIGURE 1  
DISTRIBUTION OF BLOOD GROUP GENE O IN EUROPE

blood-group frequencies uniform over the whole area, whereas there are wide variations in Western Europe in the frequencies of the ABO blood groups.

Now I want to turn to a map of Europe (Figure 1). This shows the frequencies of the O blood-group gene throughout the region. Most of the data were obtained from records of the blood transfusion services in the various countries. The point to which I want to draw your attention is the high frequency of the blood-group gene O in North-Western Europe, and particularly in the so-called Celtic countries of Scotland and Ireland. Incidentally also in North Wales, as shown by Dr. Morgan Watkin, the Welsh-speaking people taken by themselves have a high frequency of group O, but this scarcely

shows on the map, where data for the total population have been used.

The surprising thing is that the Icelanders have similar blood group frequencies to the Scots and Irish, and different ones from those found in most of modern Scandinavia, although the sagas tell us that the Vikings who colonized Iceland went from Scandinavia. There are various suggested reasons for this difference between Iceland and Scandinavia. From what we know of the rate of natural selection, it is extremely unlikely that a population like the present one of Southern Scandinavia would have altered in 800 or 900 years to what we now find in Iceland. One suggestion is that the original Icelanders came mainly from the British Isles, and only a ruling class, who wrote

# BLOOD GROUPS IN THE STUDY OF HUMAN POPULATIONS

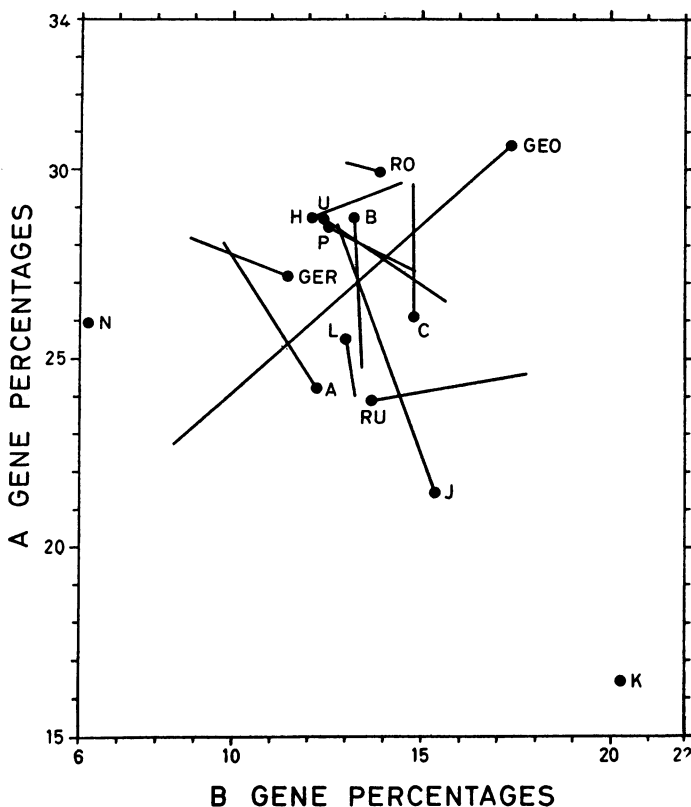


FIGURE 2  
THE A AND B GENE PERCENTAGES OF JEWS AND NON-JEWS IN EUROPE

A Austria	H Hungary	P Poland
B Byelorussia	J Jugoslavia	RO Romania
C Czechoslovakia	K Karaites	RU Russia
GEO Georgia	L Lithuania	U Ukraine
GER Germany	N Netherlands	

the sagas, came from Scandinavia. The most likely explanation, however, is that the Icelanders did indeed travel mainly from Scandinavia, but that the race which then lived on the coasts of Scandinavia was very similar to that found in Scotland and Ireland, and that the majority of present-day Scandinavians are descendants of more recent immigrants into the peninsula. We have some interesting evidence in support of this. We have known for a fairly long time that there was a rather high frequency of Group O on the west coast of Norway, and very recently it has been found that there are enclaves in Sweden with blood-group frequencies quite as extreme as those found in Iceland.

We shall next consider some people of a rather special kind, namely, the Jews. In the diagram (Figure 2) there have been plotted for a number of different populations, in the manner already described, the percentages of the A and B genes. Each of the lines on the diagram refers to a particular country of Europe: the end marked by a heavy black dot represents the Jewish population, and the other end of the line the non-Jews. We have very little information about the Jewish communities in Western Europe, so that most of the lines refer to Eastern Europe.

The points on this diagram represent mainly pre-war observations. Although the pre-war Jewish population of each of these countries

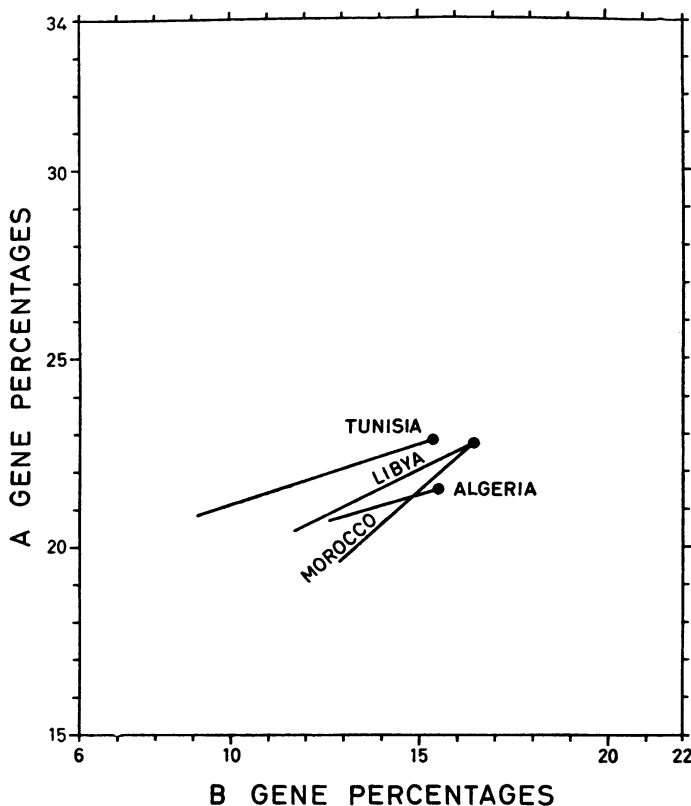


FIGURE 3

THE A AND B GENE PERCENTAGES OF JEWS AND NON-JEWS IN NORTH AFRICA

differed appreciably in average composition from the non-Jews, the average over the whole of Eastern Europe was about the same for Jews as for non-Jews, so it might be thought that there was no essential difference in blood-group frequencies and racial composition between the Jews of Eastern Europe and non-Jews. However, when the Rh groups of European Jews are studied (and unfortunately the only adequate data we have are from Jews who migrated to Canada), it is found that, while the Jews from Eastern Europe have much the same ABO blood-group frequencies as Eastern Europeans in general, their Rh groups differ quite considerably from those of the non-Jews. The Jews have a much lower frequency of Rh negatives and a higher frequency of CDe ( $R_1$ ), which would fit in with a population derived from the Eastern Mediterranean area.

While the diagram for Europe looks rather confused, that for North Africa (Figure 3) is much simpler and easier to understand. Here we see that the Jews in those North African countries for which we have adequate data represent a fairly homogeneous population. Similarly the non-Jews (Arabs in this case) are also relatively homogeneous but differ quite systematically from the Jews.

Turning to quite another part of the world, namely the Pacific area, I am sure most of you have read the book by Thor Heyerdahl in which he claimed that the Polynesians came from South America. He has subsequently written another book in which he goes into more detail, and now claims that they came in part from South America and in part from what is now Western Canada. A great many anthropologists have strongly criticized his views, but

## BLOOD GROUPS IN THE STUDY OF HUMAN POPULATIONS

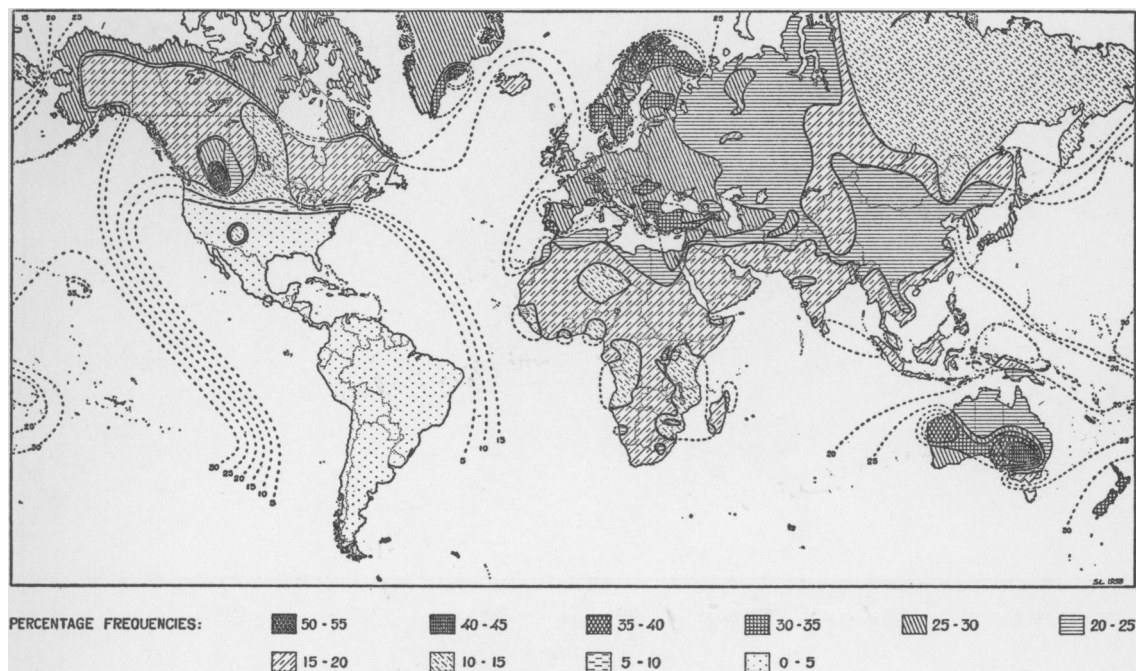


FIGURE 4

DISTRIBUTION OF BLOOD-GROUP GENE A IN THE ABORIGINAL POPULATIONS OF THE WORLD

it is interesting to see what light the blood groups throw on his theories. First of all, as regards ABO blood groups (Figure 4), the Polynesians in general are very high in blood group A and, unlike the Micronesians and Melaneseans, they are almost completely lacking in group B: in both these respects they resemble the Indians of Western Canada. But the ABO blood groups in general show such wide variations within small areas that one cannot lay too much stress on deductions from them.

However, when we come to study the Rh groups and the distribution of the Rh gene E (Figure 5) I think we are on somewhat firmer ground. Here you will see that the highest frequencies of the E gene in the world are those found in American Indians generally, particularly in Western Canada, and also, incidentally, in the Eskimos. The only other peoples who have similar E frequencies anywhere in the world are Polynesians, particularly the Maoris. One, of course, classifies the Polynesians with the American Indians in the broad group of Mongolians or Mongoloids, but this also includes

the Chinese, the Japanese, and a great many other peoples in Eastern Asia who mostly have quite low frequencies of the E gene. Actually the Japanese have rather high frequencies of E, but they also have a high incidence of B, which is lacking in American Indians and Polynesians.

Though I am far from being convinced that the Polynesians came from America (in fact, I think it is rather unlikely) I do feel that the Polynesians, from the blood group evidence, are more closely related to the American Indians than is either race to any other race in the Pacific area which has been adequately studied from the blood group point of view. We may still find, when work is done in Eastern Siberia, some evidence of a people from which they both arose, but that is speculation. I am happy to say that anthropological blood group work is now starting up in Russia again, and a certain amount of work has been done in Eastern Siberia, so that we may hope for important information on these points in the next few years.

I now want to turn to some of the differences between major races, and especially between

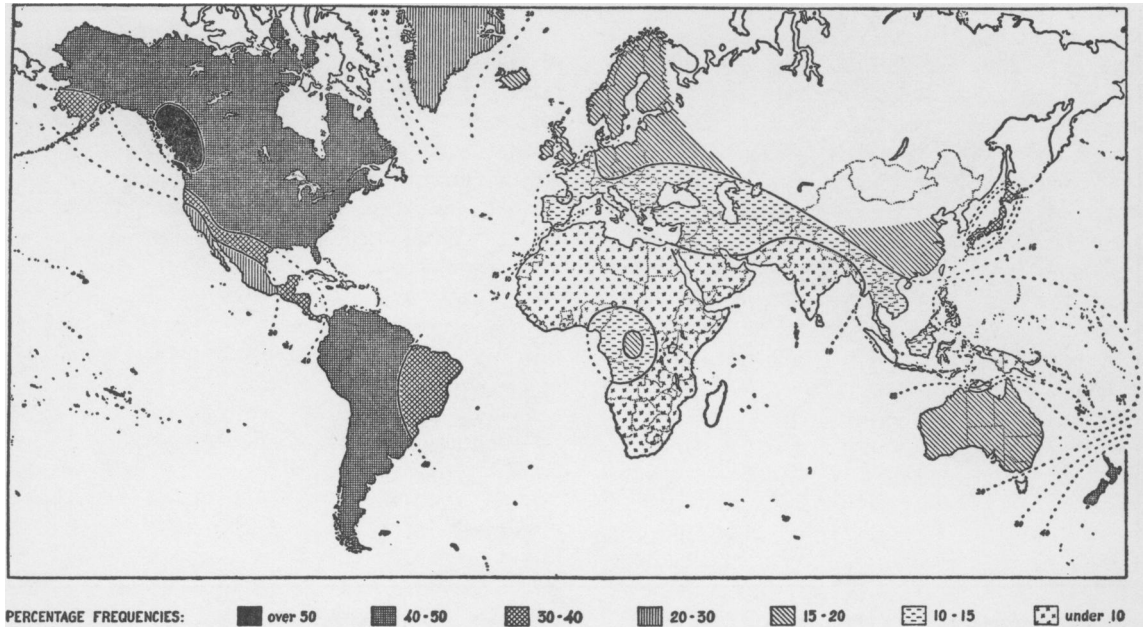


FIGURE 5

APPROXIMATE DISTRIBUTION OF THE RH BLOOD-GROUP GENE E IN THE ABORIGINAL POPULATIONS OF THE WORLD

Europeans and Africans, or rather, between Caucasoids and Negroids. Most of the basic investigations leading to our present knowledge of the blood groups have been carried out in Europe and North America using blood samples from persons of European origin. In such work blood groups cannot be recognized as such unless there are differences between individuals within the population supplying the specimens. It follows that most of the recognized blood-group systems involve differences within European populations, and that the antigens and genes discovered in this work mostly have substantial frequencies in such populations. More recently investigations have been extended to people of other races. The Japanese have for many years been active blood group workers and have, of course, investigated mainly persons of their own race, but in Europe and America a great deal of work has now been done on the blood of persons of African origin, and it has been found that there are a great many blood group antigens which are peculiar to Africans, or which have a much higher frequency in Africans than in Europeans or Mongoloids.

There are several variants in the Rh system that behave in this way, and several in the MN system. There is a third allele in the so-called Duffy blood-group system: there are only two alleles known in Europeans, but what appears to be a third allele is quite common in Africans. There is also a separate blood-group system, the Js system, where the only recognizable antigen is found almost exclusively in Africans. In contrast to this, there is only one blood group antigen, the Diego antigen, known to be a peculiar to Mongoloid peoples.

I think that one reason for the apparent divergence of the Africans is that such a lot of work has recently been done on American Negroes in America and on African Negroes in this country, but this can be only a small part of the complete explanation. It does appear as though the African races generally must have been rather long separated, genetically speaking, from the peoples of the rest of the world, and undergone their own evolution with respect to blood-group antigens.

It may be asked why you do not find the same sort of thing in Australia, since Australia is also

supposed to have been genetically and physically separated from the rest of the world for a very long time. One explanation of this may be that the aboriginal population of Australia is, and always has been, very much smaller than that of Africa. This will have two effects: firstly, that it is harder to get blood samples of Australians than of Africans, so that considerably less research has been done on them. Secondly, because of the small population there will have been much less scope for mutation. Moreover, while Africans are fairly sharply cut off from the rest of mankind, or were until comparatively recently, by the Sahara Desert, it seems that Africans within Africa have always been pretty mobile; therefore, not only will one have had relatively large numbers of mutations because of the big population; but, because of the mobility of the Africans, any of these mutations which was favoured by natural selection in the African environment will have had a chance to spread to the whole population of Africa south of the Sahara, and that is what we rather find: those genes which are almost completely confined to Africans are, in fact, found pretty well in every part of Africa, other than the extreme north. Incidentally, several of these genes are, in fact, found to a very limited extent in this country, even in perfectly blond, blue-eyed people, and it may well be that such people, as well as all the rest of us, carry genes which came out of Africa in the last 2,000 years. Ultimately, of course, all our ancestors probably came from Africa.

The other suggestion is one made recently by Professor Ruggles Gates in a talk which he gave at the Royal Anthropological Institute. He suggests the Australian aborigines are closely related to Europeans, and his evidence is that whereas in hybrid populations of European and African origin there is little or no visible segregation of the genes for skin colour, that is to say you very rarely get families consisting of some almost pure white and some almost black children from one pair of parents, you do get something approaching this in Australians; he therefore suggests that the number of colour genes by which Australian aborigines differ from Europeans is very much smaller than the number involved in the difference between

Africans and Europeans. I think a great deal more critical genetical work ought to be done on this subject. The circumstances under which Professor Gates's work had to be done in Australia were by no means as conducive to critical work as those under which Dr. Ainsworth Harrison has been able to carry out investigations on Negro-European crosses in Liverpool, from which he made the very interesting deductions which he described to this *Society* about three years ago.\* In view of the importance of the subject it is to be hoped that similar work will be done in Australia.

One could go on describing all sorts of fascinating variations in blood-group frequencies, and the deductions to be made from them, but I want to turn now to rather more general topics and see what we can deduce of a more general biological nature from the distribution of the blood groups. I want to remind you of what I said about the ABO blood groups and the Rh and MN groups, namely that you get much more rapid variation of ABO frequencies within a major region than of Rh and MN, and I suggested this was because the ABO blood groups are subject to a higher degree of natural selection. It might be suggested that the reason is really that many more people have been tested for ABO, and therefore that the variations are more apparent than real. Such a false appearance of uniformity might apply to the Duffy or Kidd groups, where relatively few tests have been done, but I think that we now have sufficient data for Rh and MN to be sure that there really is a high degree of uniformity in Western Europe, a much greater uniformity than in the case of the ABO groups.

### Blood Groups and Diseases

Sir Ronald Fisher and Dr. E. B. Ford have for many years been suggesting that the blood-group genes are subject, like all other genes, to natural selection, and that the present distribution which we find is a product of that process. Dr. Ford in particular, for about twenty years, has been urging those in a position to do so to investigate the frequencies of the various blood groups not only in the normal healthy population, but also in people suffering from a variety

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\* THE EUGENICS REVIEW, 1957, 49, 73.

of diseases, and for the whole of this time (at least twenty years) some people have been trying to do that. Unfortunately they have mostly been people working in single hospitals who have taken fifty or 100 cases of a particular disease and shown that the frequencies did not differ significantly from those found in the population as a whole.

There was one notable exception to this failure to test adequate numbers, that of the relationship between the Rh or Rhesus blood groups and haemolytic disease of the newborn, but to consider this to-night would take too long and take me too far from my main theme. So, rather reluctantly, I must leave it and continue the consideration of the relationship of other diseases to the blood groups. In the years between 1920 and 1953 there were a few rather promising individual discoveries, but the first real break through was made in the latter year by Professor Aird, Mr. Bentall and Dr. Fraser Roberts when they showed, on the basis of very large numbers, that there was a highly significant excess of blood group A in sufferers from carcinoma of the stomach. Since then, at frequent intervals, other diseases have been shown to be characterized by similar abnormal distributions of the blood groups. We find in duodenal ulcer the most striking case of all: people of group O are 1.6 times more likely to get ulcers than people of other groups; in the case of gastric ulcer, again group O is in excess, and if you are in group O you are 1.2 times more likely to have a gastric ulcer than if you are not. In the case of duodenal ulceration, and probably also for gastric ulceration, sufferers also show a higher incidence than the normal population of failure to secrete the individual's ABO blood group antigens in the saliva and other fluids. The secretion or non-secretion of these substances is determined by a pair of allelomorphous genes independent of those determining the blood groups themselves.

The diseases already mentioned are those for which a connection with blood groups is most firmly established. For certain other diseases the statistical connection appears highly significant but, because the work has been done all at one centre, or for other reasons, caution is necessary in assessing the results, and additional

evidence is desirable. The need for such caution is illustrated by a number of cases where very promising results for a particular disease at one centre or for one period have failed to be confirmed at a different centre, or for a subsequent period. It is, however, highly probable that there is an excess of group A among sufferers from diabetes mellitus, pernicious anaemia and cancer of the uterine cervix, and that there is a deficiency of O and an excess of non-secretors among cases of rheumatic carditis.

You will note that most of the conditions which I have mentioned are diseases of the gastro-intestinal tract, and that in some of them not only blood group but also secretion is involved. It looks, therefore, as though there is some connection between the nature of the gastro-intestinal or other mucous secretion and the liability to these various diseases, but it is a little difficult in most cases to explain how this connection arises.

I think it will be easier to give a plausible, though not necessarily a correct, explanation in the case of rheumatic carditis. This condition is a late effect of rheumatic fever, which is itself one effect of infection with haemolytic streptococci. One of the things for which investigators have been looking, in studying blood-group frequencies in different diseases, is significant disturbances of these frequencies in infectious diseases, since it has long been known that the blood-group antigens are closely related to antigens carried by certain bacteria. It might be expected that if you had a particular blood-group antigen on your red cells you might have difficulty in producing an antibody which would kill off bacteria which carried a similar antigen. It would then be a good thing to have as few blood-group antigens as possible, and be of group O. Therefore, one might expect a deficiency of group O in sufferers from infectious diseases, as is found in rheumatic carditis. This is, in fact, an over-simplification, since even group O people have the blood group antigen H, and since one type of haemolytic streptococcus (Type 14) carries an antigen which is related to H as well as to A and B.

### Blood Groups and Natural Selection

I want now to venture beyond the bounds of

established knowledge into speculation regarding the origin of the blood groups. We must conclude from our study of the relation between blood groups and disease that, whatever may be the precise mechanism, the blood groups are subject to natural selection in relation to the environment. In the case of duodenal ulceration an important factor is the nature of the available food, so that, if they have to eat a very rough or irritating diet, this may put the people of group O at a disadvantage to those of group A by tending more strongly to give them ulcers. In the case of other diseases the relative advantage or disadvantage of a particular blood-group may result from the bacterial environment.

So far we have considered selection only as it might affect fully evolved man. The human blood groups, however, are likely to have been inherited, in part at least, from our pre-human ancestors. We do not know what blood-group antigens were carried by those ancestors, but we may gain some clues by looking for blood groups in the lower primates, in mammals generally, and in other classes of vertebrates. Even fishes are known to have blood groups, and nearly every mammalian species that has been adequately investigated has been found to have them.

Among the anthropoid apes one finds antigens which are closely related to those of man; in the MN system in particular, an M-like antigen is present in many if not most species of primates; but as one climbs down the family tree from man through higher apes to lower monkeys, one gets more and more remote from the well-defined human pattern in the reactions of this antigen.

Another point about human beings is the enormous variety of blood-group antigens they have been shown to possess. This is certainly due in part to the fact that human beings have been very much more fully investigated than any other species of mammal, but there seems to be little doubt that a good many species of mammals have a much smaller absolute number of blood-group antigens than has man. One species of mammal which, like man, has an enormous variety of blood-group antigens is the common ox or cow, and it may be significant that cattle resemble human beings not only in

having had their blood groups very fully investigated, but also in having had great evolutionary success during the latter part of geological history. One wonders whether the ability to develop blood groups is one of the features leading to evolutionary success, or whether evolutionary success stimulates the production of blood-group antigens.

Finally, I want to mention some specific suggestions which I have previously made in an attempt to explain the origin of the blood groups; but in view of some recent discoveries in human palaeontology, I do so with even greater diffidence than hitherto. It is generally agreed that man first developed in Africa or perhaps Southern Asia. Until recently it appeared that the critical stage of evolution occurred in a relatively short space of time, geologically speaking, so that we might imagine that the earliest men, although having relatively large brains and hence the ability to make and use tools and to construct clothing and dwellings, lived at first in a similar microbiological and biochemical environment to their ape-like ancestors. However, with their ability to protect themselves from the cold and to get supplies of food, they were able to spread to other environments, and could, by means of their intelligence and use of their hands, meet the grosser harmful features of the new environments. But they came up against dangerous micro-organisms and perhaps various noxious biochemical features of the environment from which they could not protect themselves by the use of their brains and their hands, so that it was only as they evolved biochemically, developing among other things new blood groups, that they could spread effectively to all the new areas which, physically speaking, were open to them.

I have, however, been a little disturbed by some recent discoveries, for instance, that the *Australopithecines*, with their small brains, and living quite a long time ago, were already making and using simple tools: there is even a possibility that *Oreopithecus*, living in Italy at the beginning of the Pliocene, had already passed the point at which the direct line of ancestry of man had become differentiated from that of the anthropoid apes. I am not sure yet how far the ideas I have just put forward are compatible with or

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adaptable to the longer time-scale of human evolution, and the less sharp change from ape to man, that these discoveries seem to imply.

If I have not given you any firm conclusions on the more fundamental issues, I hope I have shown you how interesting the study of blood groups can be, as applied to human populations, and what valuable help they can give in tracing the history of such populations.

### REFERENCES

The facts mentioned in this talk have been drawn from many hundreds of published papers. The few works which have been cited specifically are listed below: the only way to guide the reader to the remainder is to cite a few publications, mainly of my own, which contain full bibliographies. For the basic facts of blood group distribution the following may be consulted:

Mourant, A. E. 1954. *The Distribution of the Human Blood Groups*. Oxford, Blackwell Scientific Publications.  
Mourant, A. E., Kopec, Ada C. and Domaniewska-Sobczak, Kazimiera. 1958. *The ABO Blood Groups: Comprehensive Tables and Maps of World Distribution*. Oxford, Blackwell Scientific Publications.

More recent facts are set out and discussed in three papers published in the *British Medical Bulletin*, May 1959: 15, Pt. 2.

Roberts, J. A. F. Blood Groups and Disease. 129-133.  
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